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Research paper

A comparative analysis of the spatio-temporal variation in the phenologies of two herbaceous species and associated climatic driving factors on the Tibetan Plateau

Wenquan Zhu[a,b,c,*,1], Zhoutao Zheng[a,b,c,*,1], Nan Jiang[a,b,c], Donghai Zhang[a,b,c]

[a] State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing, 100875, China
[b] Joint Center for Global Change Studies (JCGCS), Beijing, 100875, China
[c] Beijing Engineering Research Center for Global Land Remote Sensing Products, Institute of Remote Sensing Science and Engineering, Faculty of Geographical Science, Beijing Normal University, Beijing, 100875, China

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ABSTRACT

Studying the differences in phenology among plant species is important for understanding their physiological and reproductive responses to climate change and complex inter-species interactions. This study conducted a comparative analysis of the spatio-temporal variation in the phenologies of two herbaceous species (*Plantago asiatica* and *Taraxacum mongolicum*) and associated climatic driving factors on the Tibetan Plateau (TP) based on ground-observed phenology data during 2000–2012. The results indicated that both spring and autumn phenology of the two species showed strong dependences on altitude, latitude and longitude, although the magnitudes of the variation with geographical factors were different among species. Change in altitude contributed the most to the spatial variation in phenology for both species. In addition, strong dependences on altitude were also observed for the phenological differences between the two species. With the increase of altitude, the same phenophases of the two species tended to occur synchronously at first and then the chronological order of the same phenophases between the two species changed. Spring and autumn phenophases showed significant negative correlations with the growing degree-days (GDD) and the cold degree-days (CDD) ($p < 0.001$), respectively. Moreover, the phenophases of *T. mongolicum* were more sensitive than those of *P. asiatica* in response to GDD or CDD, which explained the spatial variation in the phenological difference between the two species. The divergent phenological responses to climate change and the spatial variation in phenological differences between *P. asiatica* and *T. mongolicum* may alter the inter-species interactions between the two species.

1. Introduction

Plant phenology is the study of the timing of recurring biological events of plant developmental stages caused by biotic and abiotic factors, including the occurrence of leafing, flowering and fruiting (Lieth, 1974; Morisette et al., 2009). Plant phenology is sensitive to changes in climate and the natural environment (Cong et al., 2012; Morisette et al., 2009). Moreover, it plays a crucial role in regulating the exchange of the fluxes of water, CO_2 and energy between the biosphere and atmosphere (Keenan et al., 2012; Richardson et al., 2012; Richardson et al., 2013). Shifts in phenology can reflect the adjustments and responses of the biosphere to climate change (Penuelas and Filella, 2001). Therefore, plant phenology has received extensive attention in the field of global change in recent years (Menzel, 2002).

Global warming has altered plant phenology in recent decades (Menzel et al., 2006; Parmesan and Yohe, 2003; Root et al., 2003). Many studies have reported advanced spring phenology and delayed autumn phenology worldwide, which has resulted in an extended growing season (Jeong et al., 2011; Menzel, 2000; Piao et al., 2006; Zhu et al., 2012). However, the phenological shifts vary in response to climate change at different locations, even for the same species (Primack et al., 2009; Schwartz and Hanes, 2010), and different species within the same community may also show distinct responses (Cleland et al., 2006; Crimmins et al., 2010; Diez et al., 2012; Fitter and Fitter, 2002; Miller-Rushing and Primack, 2008). Moreover, different changes in phenology among species could lead to alterations in inter-species relationships (Stenseth and Mysterud, 2002; Visser and Both, 2005), potentially altering the community structure and function (Richardson

* Corresponding authors at: Institute of Remote Sensing Science and Engineering, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China.
E-mail addresses: zhuwq75@bnu.edu.cn (W. Zhu), zhengzt90@mail.bnu.edu.cn (Z. Zheng).
[1] These authors contributed equally to this work.

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et al., 2013). For example, Fitter and Fitter (2002) found that due to the different responses in flowering of 6 pairs of species that can form natural hybrids in the vicinity of a single locality in south-central England, 4 pairs of species were more likely to flower synchronously than they were formerly, increasing the probability of hybridization, and 2 were less likely to, reducing the probability of hybridization.

Plant phenology is much more sensitive to climate change on the Tibetan Plateau (TP) due to its harsh physical environment; this region is commonly known as Earth's "third pole". The unique geographical and environmental backgrounds make the TP an ideal region to explore the potential changes in plant communities under climate change by studying inter-species differences in phenological responses. Through experimental warming in a typical alpine meadow on the TP during 2014–2015, Zhu et al. (2016) found that warming caused the convergence of the flowering events of early- and late-flowering species and increased the overlap period of flowering among species, which could alter the competitive relationships among species. However, existing studies about inter-species differences in phenological responses to climate change on the TP to date have mainly focused on a single site with a few years' records, and a comparative analysis of the spatio-temporal variation in phenology based on multi-site and multi-year phenological records is therefore lacking.

Thanks to the phenology network established by the China Meteorological Administration, a large number of continuous and long-term, ground-observed phenology records across the TP can be available. At present, 26 phenological stations are distributed on the TP, with 22 herbaceous plants and 10 woody plants observed (Zheng et al., 2016). However, only two perennial herbs, herba plantaginis (*Plantago asiatica*, Plantaginaceae family) and dandelion (*Taraxacum mongolicum*, Compositae family), were widely observed among all stations. Focusing on the two species, this study aims to reveal the inter-species differences in phenological responses to climate change and the associated climatic driving factors on the TP.

2. Data and methods

2.1. Phenological dataset

The phenological data for *P. asiatica* and *T. mongolicum* on the TP were collected from the nation-wide phenological observation network established by the China Meteorological Administration. The starting year for the phenological records of the two species differed among stations and species. For example, the phenology of *P. asiatica* began to be recorded in 1983 at Huangyuan and Zoige stations, while that of *T. mongolicum* only started to be recorded in 2002 at Shiqu station. On the other hand, phenological observations continued at all stations except Maqu station, at which the observations discontinued after 2009. The phenological data for the two species during 2000–2012 were selected in this study because they were generally almost available during this period at the corresponding stations. Moreover, the key phenological metrics of the first leaf date (FLD), first flowering date (FFD), common leaf coloring date (LCD) and length of the growing season (LOG) were selected. FLD is defined as the date when a few leaves are fully expanded, FFD is defined as the date when a few flowers are fully blooming, and LCD is defined as the date when more than 50% of the green leaves have turned yellow (China Meteorological Administration, 1993). The time between FLD and LCD is regarded as LOG. All the onset dates of FLD, FFD and LCD were converted to the Julian day of year (DOY).

Outliers were removed from the phenological data according to the 30-day rule as proposed by Schaber and Badeck (2002). For each phenological metric, only the time series with at least 10-years records existed during 2000–2012 were included in the analysis. Finally, 16 phenological stations were selected for this study (Fig. 1). The phenology of each species was observed at 13 stations individually. Meanwhile, there were 10 stations recording the phenologies of the two species concurrently. More details about the locations and the plant species observed at each station can be found in Table S1 in Supplement A.

2.2. Climate dataset

The meteorological data were obtained from the China Meteorological Data Service System (http://data.cma.cn/), including the daily mean air temperature and daily precipitation at 96 stations on the TP from 2000 to 2012. Because daily meteorological data were not available for Haiyan, Huangyuan, Huzhu and Gande stations, the ANUSPLIN 4.3 software (Hutchinson, 2004), combined with the Digital Elevation Model (DEM) data derived from the US Geological Survey, was used to interpolate the daily mean air temperature and daily precipitation into 1 km × 1 km grids over the study region. Thus, gridded daily mean air temperature and daily precipitation data at the 4 phenological stations without daily meteorological data were obtained.

2.3. Frequency statistics for the occurring time of phenophases

To depict the phenological metrics, the mean, median, minimum, maximum, 25th and 75th percentiles for each phenological metric (FLD, FFD, LCD and LOG) across all stations over 2000–2012 were calculated for each species and exhibited by the boxplots. Meanwhile, the distributions of the differences in FLD (ΔFLD), FFD (ΔFFD), LCD (ΔLCD) and LOG (ΔLOG) between *P. asiatica* and *T. mongolicum* across all stations with both species observed over 2000–2012 were also illustrated by the boxplots.

2.4. Analysis of the spatial and temporal variations in phenological metrics

To explore the effect of geographical factors and years on the spatial-temporal variations in the phenological metrics (FLD, FFD, LCD and LOG) and the phenological differences (ΔFLD, ΔFFD, ΔLCD and ΔLOG) between *P. asiatica* and *T. mongolicum*, the stepwise multiple linear regression model was performed with geographical factors (longitude, latitude and altitude) and year as independent variables. The variance inflation factor (VIF) was used to detect the multi-collinearity among variables in the models. Models were accepted only if the VIF of individual predictors was less than 3, which indicated no multi-collinearity (Zuur et al., 2010). The squared semi-partial correlation coefficients were used to quantify the relative contribution of each independent variable in a given model, which were determined as the reduction in R^2 with removing a given predictor from the set of independent variables (Watson et al., 2011).

2.5. Analysis of the relationships between climatic driving factors and phenology

The growing degree-days (GDD) has been widely used as a measure of heat accumulation to assess the effect of temperature on spring phenophases (Chuine, 2000; Fu et al., 2014; Shen et al., 2015). On the other hand, the cold degree-days (CDD), as a surrogate for cumulative heat deficit, has been adopted to explain the variation in autumn phenophases (Delpierre et al., 2009; Dragoni and Rahman, 2012; Richardson et al., 2006). GDD was calculated as the thermal sum of the difference between daily mean temperature (T_m) and the base temperature (T_b) between DOY_1 and DOY_2 (Eq. (1)).

$$GDD = \sum_{DOY_1}^{DOY_2} \begin{bmatrix} (T_m - T_b) & when & T_m > T_b \\ 0 & when & T_m \le T_b \end{bmatrix} \quad (1)$$

Here, T_b was set to be 0 °C; DOY_1 was set as 1st January. To analyze the correlation between phenology and GDD across different stations and years, the end dates of GDD should be set to fixed dates. Specifically, DOY_2 was set to 30th April and 30th June for FLD and FFD,

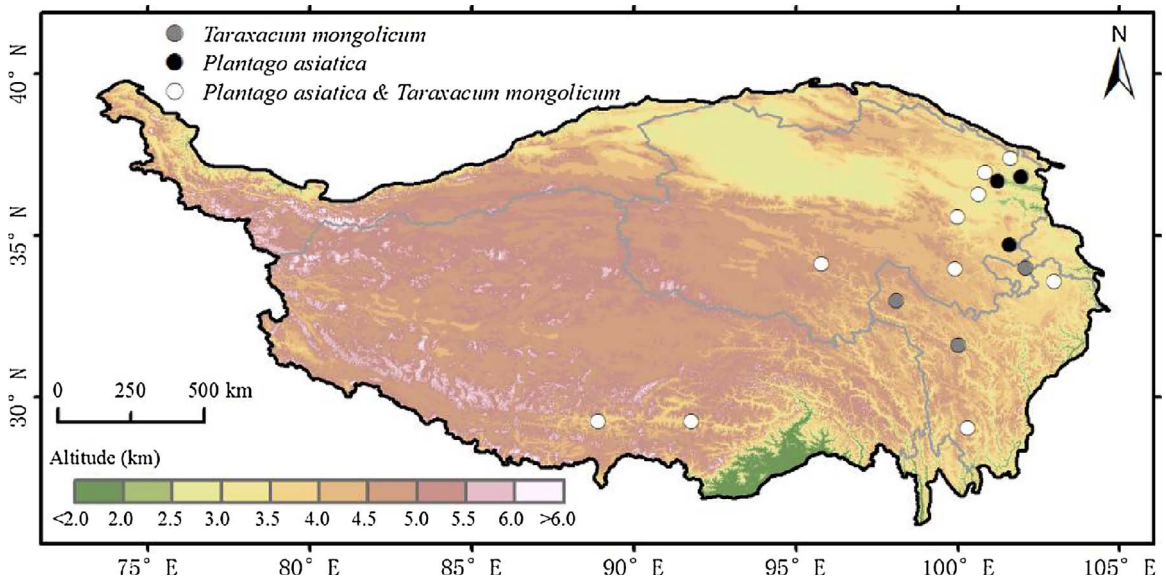

Fig. 1. The distribution of phenological stations with *Plantago asiatica* and/or *Taraxacum mongolicum* observed on the Tibetan Plateau.

respectively. GDD_{FLD} and GDD_{FFD} represented the GDD of FLD and FFD, respectively. The base temperature of 5 °C and 10 °C was also tested, and very similar results were observed. Therefore, only the results using the base temperature of 0 °C for GDD were reported in this study.

CDD was calculated as the sum of the difference between the base temperature (T_b) and daily mean temperature (T_m) between DOY_1 and DOY_2 (Eq. (2)).

$$CDD = \sum_{DOY_1}^{DOY_2} \begin{bmatrix} (T_b - T_m) & when \quad T_b > T_m \\ 0 & when \quad T_b \le T_m \end{bmatrix} \tag{2}$$

Here, T_b was set to be 15 °C; DOY_1 was set as 1st August. Similar to the calculation of GDD, the end dates of CDD were also fixed. Specifically, DOY_2 was set to 31st October. CDD_{LCD} represented the CDD of LCD. The base temperature of 10 °C and 20 °C was also tested, and very similar results were observed. Therefore, only the results using the base temperature of 15 °C for CDD were reported in this study.

The accumulated precipitation (PPT) during the same periods as GDD or CDD was also calculated for different phenophases. Then the partial correlation method was used to analyze the climate controls on the phenophases across all stations and years. At last, simple regression analyses were conducted between climatic factors and phenophases to quantify the effects of climatic factors on the phenophases.

The statistical significance of all the regression coefficients and correlation coefficients was examined using the *F*-test in this study. *P* values less than 0.05 were considered significant.

3. Results

3.1. Occurring time of phenophases

The mean FLD and LCD of *P. asiatica* occurred at DOY 103 and 284, respectively, resulting in a mean LOG of 181 days (Fig. 2). Meanwhile, the mean FLD, LCD and LOG of *T. mongolicum* were very close to the mean value of corresponding phenological metrics of *P. asiatica*. However, the median and the mean value of FFD were 10.50 and 11.15 days earlier for *T. mongolicum* than *P. asiatica*, respectively. In addition, the phenological metrics varied more for *T. mongolicum* than *P. asiatica* as shown by a higher spread of percentiles and larger ranges (maximum − minimum) in Fig. 2. The median as well as the mean value of differences in phenological metrics between the two species were close to 0 except for FFD (Fig. 3). The median and the mean value of ΔFFD were 18.00 and 17.41 days, respectively.

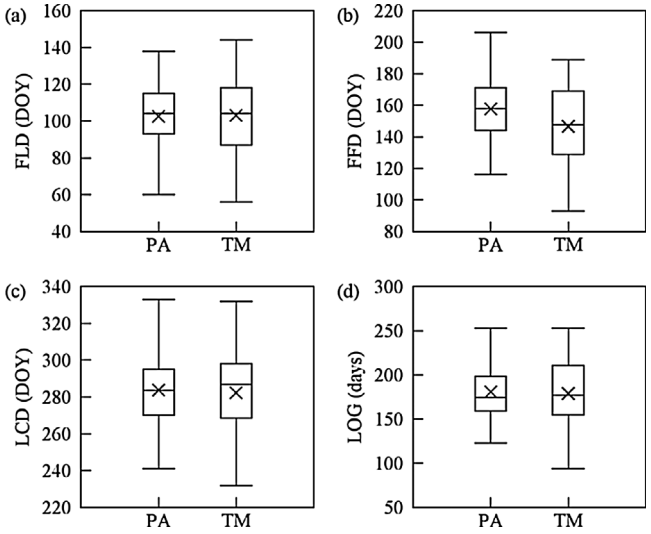

Fig. 2. The distribution of (a) first leaf date (FLD), (b) first flowering date (FFD), (c) common leaf coloring date (LCD) and (d) length of the growing season (LOG) for *Plantago asiatica* and *Taraxacum mongolicum* across all stations over 2000–2012. The bottoms and tops of boxes are the 25th and 75th percentiles; the bands near the middle are the median; the ends of the whiskers represent the minimum and maximum; and the crosses designate the mean value. PA and TM indicate *P. asiatica* and *T. mongolicum*, respectively. DOY indicates the Julian day of year.

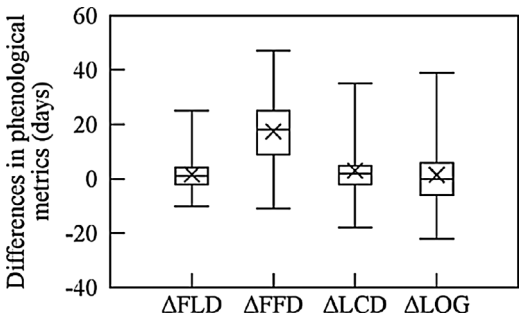

Fig. 3. The distribution of phenological differences (*Plantago asiatica* − *Taraxacum mongolicum*) across all stations with both species observed over 2000–2012. ΔFLD, ΔFFD, ΔLCD and ΔLOG indicate the difference in first leaf date, first flowering date, common leaf coloring date and length of growing season between *Plantago asiatica* and *Taraxacum mongolicum*, respectively. See Fig. 2 for the descriptions about the boxplot.

Table 1
Stepwise multiple linear regression coefficients of each independent variable related to phenological metrics across the Tibetan Plateau.

Species	Phenological metric	Longitude (days $^{\circ -1}$)	Latitude (days $^{\circ -1}$)	Altitude (days km^{-1})	Year (days yr^{-1})	N	R^2
Plantago asiatica	FLD	1.07(0.03)***	5.84(0.38)***	29.95(0.46)***	N/A	167	0.80***
	FFD	1.66(0.07)***	4.68(0.22)***	36.38(0.62)***	N/A	166	0.78***
	LCD	−2.22(0.13)***	−2.89(0.09)***	−18.54(0.17)***	N/A	166	0.49***
	LOG	−3.27(0.09)***	−8.69(0.26)***	−48.34(0.37)***	N/A	166	0.76***
Taraxacum mongolicum	FLD	1.75(0.07)***	5.56(0.29)***	45.68(0.64)***	N/A	158	0.86***
	FFD	2.76(0.13)***	4.43(0.15)***	49.60(0.61)***	N/A	158	0.78***
	LCD	−2.33(0.10)***	−4.61(0.17)***	−49.33(0.63)***	0.67(0.01)**	157	0.78***
	LOG	−4.09(0.09)***	−10.20(0.25)***	−95.05(0.71)***	N/A	157	0.89***

FLD, FFD, LCD and LOG indicate the first leaf date, first flowering date, common leaf coloring date and length of growing season, respectively. Numbers in brackets indicate the squared semi-partial correlation coefficients. N indicates the number of phenological records. * indicates $p < 0.05$; ** indicates $p < 0.01$; and *** indicates $p < 0.001$. Missing estimates (N/A) are not significant.

3.2. Spatial variation in phenology

Based on the results from the multiple regression analysis, the spring phenophases showed a significant positive correlation with geographical factors (longitude, latitude and altitude) for both *P. asiatica* and *T. mongolicum* ($p < 0.001$) (Table 1). Both FLD and FFD of *P. asiatica* occurred later with increasing longitude (1.07 and 1.66 days per degree), latitude (5.84 and 4.68 days per degree) and altitude (29.95 and 36.38 days per kilometer). The geographical factors could explain 80% and 78% of the spatial variation in FLD and FFD for *P. asiatica*, respectively. Compared with *P. asiatica*, *T. mongolicum* showed a larger absolute value of regression coefficient for each geographical factor related to spring phenology except for latitude (Table 1). FLD and FFD of *T. mongolicum* occurred 1.75 and 2.76 days later per degree of longitude from west to east, 5.56 and 4.43 days later per degree of latitude from south to north and 45.68 and 49.60 days later per kilometer of altitude from low to high, respectively. The geographical factors could explain 86% and 78% of the spatial variation in FLD and FFD for *T. mongolicum*, respectively.

Contrary to the spring phenophases, the autumn phenophases were significantly negatively correlated with geographical factors for both species ($p < 0.001$) (Table 1). LCD of *P. asiatica* occurred earlier with the increase of longitude (2.22 days per degree), latitude (2.89 days per degree) and altitude (18.54 days per kilometer). Moreover, stronger dependences of the LCD on geographical factors were found for *T. mongolicum*. LCD of *T. mongolicum* advanced 2.33 days for every degree eastward, 4.61 days for every degree northward and 49.33 days for every kilometer increase in altitude.

Due to the dependences of FLD and LCD on geographical factors, LOG shortened 3.27 and 4.09 days per degree of longitude from west to east, 8.69 and 10.20 days per degree of latitude from south to north and 48.34 and 95.05 days per kilometer greater altitude for *P. asiatica* and *T. mongolicum*, respectively ($p < 0.001$) (Table 1). In addition, all phenological metrics showed stronger dependences on latitude than on longitude for both species. The geographical factors were able to account for 76% and 89% of the variation in the LOG for *P. asiatica* and *T. mongolicum*, respectively.

Moreover, altitude had the largest contribution to the spatial variation in all phenological metrics as indicated by the largest squared semi-partial correlation coefficients (Table 1). In comparison, the contribution of longitude was weaker than that of latitude to the spatial variation in the same phenological metrics except for LCD of *P. asiatica* (Table 1).

Across all the stations with both species observed, the differences in phenological metrics between *P. asiatica* and *T. mongolicum* also showed significant relationships with geographical factors (Table 2). Especially, the squared semi-partial correlation coefficients of altitude were much larger than those of the other factors, which meant altitude was the most important variable to the phenological difference among the explanatory variables. With the increase of altitude, ΔFLD and ΔFFD decreased 8.03 and 13.91 days per kilometer, respectively, whereas ΔLCD and ΔLOG increased 13.28 and 20.29 days per kilometer, respectively. Due to the strong dependence of phenological differences on altitude, the phenological sequence of FLD as well as LCD between the two species changed with the increase of altitude (Fig. 4a, c). In low altitudes, FLD of *P. asiatica* occurred later than that of *T. mongolicum* (indicated by positive ΔFLD) (Fig. 4a). With the increase of altitude, FLD of *P. asiatica* tended to occur synchronously with that of *T. mongolicum* at first but would occur earlier than that of *T. mongolicum* at last (Fig. 4a), while LCD between the two species showed an opposite change direction in phenological sequence (Fig. 4c). As a result, LOG of *P. asiatica* was shorter than that of *T. mongolicum* in low latitudes but longer in high altitudes (Fig. 4d).

3.3. Temporal variation in phenology

No significant temporal trends were found in the phenological metrics except for LCD of *T. mongolicum*, which delayed at a rate of 0.67 days per year during 2000–2012 ($p < 0.01$) (Table 1). Regarding the temporal trends in the differences in phenological metrics, ΔLCD and ΔLOG decreased significantly at rates of 0.44 ($p < 0.05$) and 0.61 ($p < 0.01$) days yr^{-1} during 2000–2012, respectively (Table 2). However, ΔFLD and ΔFFD showed no significant temporal trends.

3.4. The relationships between phenology and climatic driving factors

Significant negative partial correlations ($p < 0.001$) were found between spring/autumn phenological metrics and GDD/CDD across all stations and years for both species (Table 3). In contrast, the correlations between phenological metrics and PPT were extremely weak after removing the effect of GDD/CDD in the partial correlation analysis. The phenophases of *T. mongolicum* were more sensitive than those of *P. asiatica* in response to GDD/CDD (Fig. 5). With an increase of 100 °C-days in GDD_{FLD}, FLD occurred 7.8 and 9.1 days earlier for *P. asiatica* and *T. mongolicum*, respectively (Fig. 5a, b), while the same increase in GDD_{FFD} initiated FFD about 3.8 and 4.9 days earlier for *P. asiatica* and *T. mongolicum*, respectively (Fig. 5c, d). With regard to autumn phenology, LCD occurred 4.3 and 6.8 days earlier for every 100 °C-days increase in CDD_{LCD} for *P. asiatica* and *T. mongolicum*, respectively (Fig. 5e, f). The phenological sensitivities to GDD/CDD were also stronger for *T. mongolicum* than *P. asiatica* across the 10 stations with both species observed (Fig. S1 in Supplement A).

4. Discussion

4.1. Inter-species differences in the effect of geographical factors on the spatial distributions of phenology

Similar spatial distributions of phenology were observed between *T. mongolicum* and *P. asiatica*, although the magnitudes of the spatial

Table 2
Stepwise multiple linear regression coefficients of each independent variable related to the differences in the phenological metrics between *Plantago asiatica* and *Taraxacum mongolicum* across the Tibetan Plateau.

Differences in phenological metric	Longitude (days $^{\circ -1}$)	Latitude (days $^{\circ -1}$)	Altitude (days km^{-1})	Year (days yr^{-1})	N	R^2
ΔFLD	N/A	N/A	−8.03(0.37)***	N/A	126	0.37***
ΔFFD	N/A	−1.14 (0.07)**	−13.91(0.20)***	N/A	125	0.20***
ΔLCD	0.55(0.04)*	0.73(0.03)*	13.28(0.26)***	−0.44(0.03)*	124	0.32***
ΔLOG	0.95(0.09)***	N/A	20.29(0.45)***	−0.61(0.03)**	124	0.50***

ΔFLD, ΔFFD, ΔLCD and ΔLOG indicate the difference in first leaf date, first flowering date, common leaf coloring date and length of growing season between *Plantago asiatica* and *Taraxacum mongolicum*, respectively. Numbers in brackets indicate the squared semi-partial correlation coefficients. N indicates the number of phenological records. * indicates $p < 0.05$; ** indicates $p < 0.01$; and *** indicates $p < 0.001$. Missing estimates (N/A) are not significant.

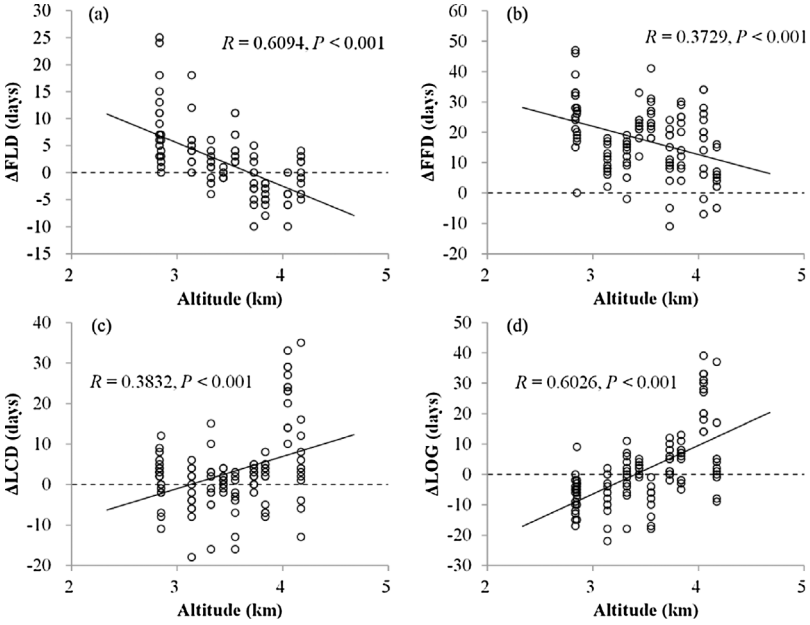

Fig. 4. The relationship between the phenological difference (*Plantago asiatica* − *Taraxacum mongolicum*) and altitude with regard to (a) first leaf date (FLD), (b) first flowering date (FFD), (c) common leaf coloring date (LCD) and (d) length of the growing season (LOG) across the Tibetan Plateau.

Table 3
Partial correlation coefficients between the phenological metrics and climatic factors across all stations and years.

Species	Phenological metric	GDD	CDD	PPT	N
Plantago asiatica	FLD	−0.793***	\	−0.061	167
	FFD	−0.781***	\	0.042	166
	LCD	\	−0.605***	0.092	166
Taraxacum mongolicum	FLD	−0.805***	\	0.043	158
	FFD	−0.760***	\	0.108	158
	LCD	\	−0.771***	−0.022	157

FLD, FFD and LCD indicate the first leaf date, first flowering date and common leaf coloring date, respectively. GDD, CDD and PPT indicate the growing degree-days, cold degree-days and accumulated precipitation, respectively. All climatic factors (GDD, CDD and PPT) for FLD, FFD and LCD were calculated based on daily meteorological data from 1st January to 30th April, from 1st January to 30th June and from 1st August to 31st October, respectively. N indicates the number of phenological records. *** indicates $p < 0.001$.

variation with geographical factors were different. All phenological metrics for both species showed a strong dependence on geographical factors. Specifically, increasing latitude, longitude and altitude will lead to later spring phenology (FLD and FFD), earlier autumn phenology (LCD) and shorter growing season (LOG). Therefore, the spatial distributions of phenology for *P. asiatica* and *T. mongolicum* on the TP were consistent with the Hopkins' Bioclimatic Law, which describes phenology as varying along climatic gradients by latitude, longitude, and altitude (Hopkins, 1918). Strong dependences of phenology on geographical factors were also widely observed in other regions of the Northern Hemisphere (Dai et al., 2014; Rötzer and Chmielewski, 2001; Wang et al., 2015). However, on the TP, altitude was the most important variable to the spatial variation in phenology while the contribution of longitude and latitude was much weaker for both species (Table 1). The weak but significant relationship between longitude and phenology was probably due to the mass elevation effect of TP (de Quervain, 1904; Zhang et al., 2016), which led to a decreasing temperature gradient from the inner (low longitudes in the west) to the outer (high longitudes in the east) parts of the plateau at the same elevation (Yao and Zhang, 2015). Moreover, an interesting finding is that the variations in autumn phenology on the TP could be well explained by the geographical factors (especially for *T. mongolicum*), contrary to the relatively unclear relationships between autumn phenology and environmental factors in other regions (Gallinat et al., 2015).

4.2. Inter-species differences in the spatial variation in phenology

Due to the strong dependence of phenological differences on altitude, the phenological sequence of FLD as well as LCD between *P. asiatica* and *T. mongolicum* had changed with the increase of altitude (Table 2, Fig. 4). In low altitudes with a warm environment, FLD occurred later while LCD occurred earlier for *P. asiatica* than *T. mongolicum* (Fig. 4a, c). However, opposite phenological sequence in FLD as well as LCD was found in high altitudes with a cold environment (Fig. 4a, c). These findings implied that the phenological sequence between the two species in the same community may change with climate warming in the future. Usually, the chronological order of phenophases between different plant species is thought to be stable

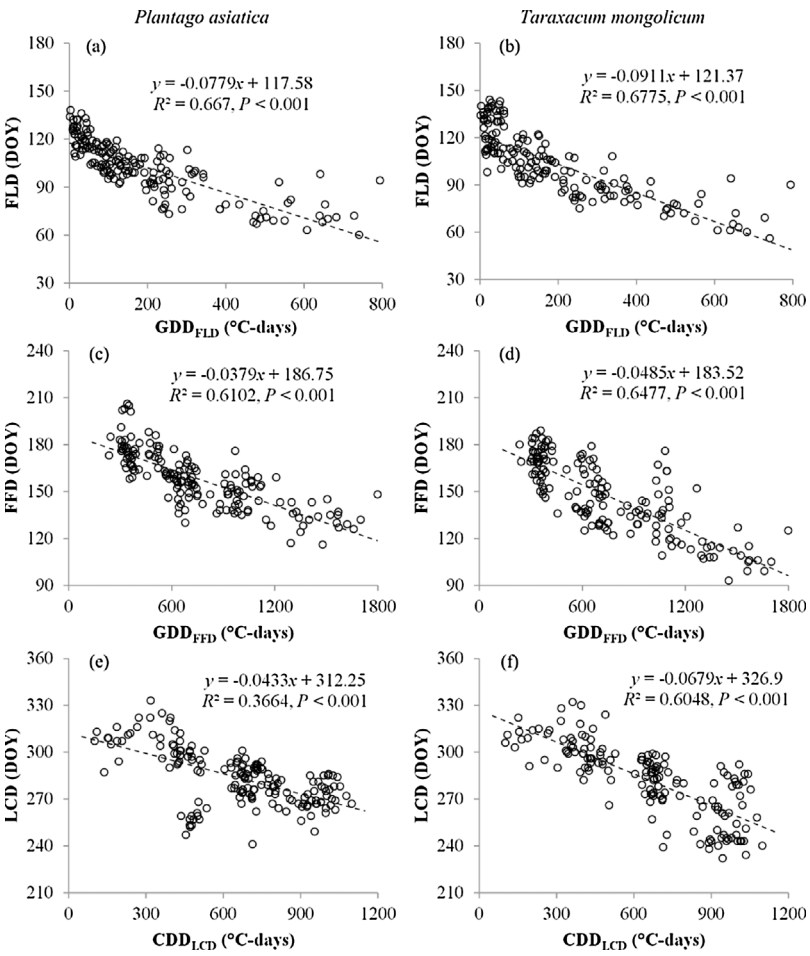

Fig. 5. The relationship between the onset dates of phenophases and growing degree-days/cold degree-days (GDD/CDD) across all stations and years for *Plantago asiatica* (a, c and e) and *Taraxacum mongolicum* (b, d and f). FLD, FFD and LCD indicate the first leaf date, first flowering date and common leaf coloring date, respectively. DOY indicates the Julian day of year.

(Wesolowski and Rowinski, 2006), but substantial changes in the chronological order of species' budburst resulting from lack of chilling were found in a climate chamber experiment (Laube et al., 2014), which was consistent with our findings based on field data.

Changes in plant phenology result from the adjustment and adaptation of plants to climate and environmental change. Different adaptations of the species within a community will determine the capacity of inter-species competition, which may alter the inter-species interactions and even the structure and function of an ecosystem (Cleland et al., 2007; Fitter and Fitter, 2002; Walther et al., 2002). Therefore, inter-species competition was strongly influenced by phenological sequence in a community. Change in phenological sequence in a community may induce competition for limited resources and subsequently alter the inter-species interactions. In this study, FLD (LCD) of *T. mongolicum* occurred later (earlier) than that of *P. asiatica* in high altitudes with a colder climate, while occurred earlier (later) in low altitudes with a warmer climate (Fig. 4a). Therefore, FLD and LCD of *T. mongolicum* in high altitudes may tend to occur synchronously with that of *P. asiatica* if climate becomes warmer in the future, resulting in a more intensive inter-species competition for water, nutrient and light. However, further research is needed to detect the influence of inter-species interactions resulted from the change of phenological sequence between *P. asiatica* and *T. mongolicum* growing in the same community on the TP through field experiment.

4.3. Inter-species differences in climatic factors driving the spatial variation in phenology

Significant negative partial correlations ($p < 0.001$) were observed between spring/autumn phenophases and GDD/CDD across all stations and years for both species. However, *T. mongolicum* showed a more sensitive response of spring/autumn phenophases to GDD/CDD than *P. asiatica*. More thermal accumulation tended to advance the occurrence of spring phenophases while less heat deficit could result in a delay of autumn phenophases for both species (Table 3 and Fig. 5). Previous studies have shown that temperature is an important factor influencing spring phenology in temperate and boreal regions (Chuine et al., 2000; Jeong et al., 2011; Menzel et al., 2006; Parmesan and Yohe, 2003; Root et al., 2003). Notably, some studies have shown that spring phenology is negatively correlated with the preseason temperature on the TP (Piao et al., 2011; Zheng et al., 2016), which was consistent with our findings in this study. For autumn phenology, previous studies have shown that cumulative cold temperatures below a certain threshold trigger leaf senescence (Delpierre et al., 2009; Dragoni and Rahman, 2012; Gill et al., 2015; Richardson et al., 2006). It also means that warm temperature in autumn can lead to a delay of autumn phenology (Jeong et al., 2011; Zeng et al., 2011). However, autumn phenology was found to be weakly linked to autumn temperature in many studies (e.g., Dai et al., 2014; Gallinat et al., 2015). By contrast, our study showed a high correlation between autumn phenology and CDD for both species on the TP. Besides, the delay of autumn phenology resulting from warm temperature on the TP could also be found in other studies based on remote sensing data. Yu et al. (2010) found that the end of growing season (EGS) was delayed with increasing temperature in September for alpine meadow during 1982–2006. Che et al. (2014) also found that the spatial distribution of the EGS was significantly positively correlated with both monthly temperature of August and September across 46 meteorological stations during 1982–2011.

The relationship between precipitation and spring/autumn phenophases was weak for both species in our study. Previous studies

reported that the influence of precipitation on green-up date was strong in arid areas but weak in wet areas on the TP (Shen et al., 2011; Zhang et al., 2015). Sufficient soil moisture could be available across the phenology stations on the TP due to the snowmelt supplies. Moreover, the temporal distribution in precipitation, rather than the total, may be more associated with plant phenology (Dragoni and Rahman, 2012).

5. Conclusions

Based on ground-observed phenology data on the Tibetan Plateau (TP) during 2000–2012, this study conducted a comparative analysis of the spatio-temporal variation in phenology and associated climatic driving factors for two herbaceous plants (*Plantago asiatica* and *Taraxacum mongolicum*). Strong dependence on geographical factors was observed for spring and autumn phenological metrics of both species. Change in altitude contributed the most to the spatial variation in phenology for both species. The spatial variations in the differences in phenological metrics between the two species were also strongly dependent on altitude. With the increase of altitude, the same phenophases of the two species tended to occur synchronously at first and then the chronological order of the same phenophases between the two species changed. In low altitudes with a warm climate, the first leaf date occurred later while the common leaf coloring date occurred earlier for *P. asiatica* than *T. mongolicum*. However, opposite phenological sequence in the first leaf date as well as the common leaf coloring date was found in high altitudes with a cold climate. Temperature was the main driver of the spatio-temporal variation in the phenologies of *P. asiatica* and *T. mongolicum* on the TP. Spring phenophases showed a significant negative correlation with the growing degree-days (GDD) while autumn phenophases showed a significant negative correlation with the cold degree-days (CDD) ($p < 0.001$). However, the relationships between precipitation and spring/autumn phenophases were weak for both species. Moreover, the phenophases of *T. mongolicum* were more sensitive than those of *P. asiatica* in response to GDD or CDD, which explained the spatial variation in the phenological difference between the two species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.09.021.

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